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Fire-driven vegetation type conversion in Southern California

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Abstract
One consequence of global change causing widespread concern is the possibility of ecosystem conversions from one type to another. A classic example of this is vegetation type conversion (VTC) from native woody shrublands to invasive annual grasslands in the biodiversity hotspot of Southern California. Although the significance of this problem is well recognized, understanding where, how much, and why this change is occurring remains elusive owing to differences in results from studies conducted using different methods, spatial extents, and scales. Disagreement has arisen particularly over the relative importance of short-interval fires in driving these changes. Chronosequence approaches that use space for time to estimate changes have produced different results than studies of changes at a site over time. Here we calculated the percentage woody and herbaceous cover across Southern California using air photos from ~1950 to 2019. We assessed the extent of woody cover change and the relative importance of fire history, topography, soil moisture, and distance to human infrastructure in explaining change across a hierarchy of spatial extents and regions. We found substantial net decline in woody cover and expansion of herbaceous vegetation across all regions, but the most dramatic changes occurred in the northern interior and southern coastal areas. Variables related to frequent, short-interval fire were consistently top ranked as the explanation for shrub to grassland type conversion, but low soil moisture and topographic complexity were also strong correlates. Despite the consistent importance of fire, there was substantial geographical variation in the relative importance of drivers, and these differences resulted in different mapped predictions of VTC. This geographical variation is important to recognize for management decision-making and, in addition to differences in methodological design, may also partly explain differences in previous study results. The overwhelming importance of short-interval fire has management implications. It suggests that actions should be directed away from imposing fires to preventing fires. Prevention can be controlled through management actions that limit ignitions, fire spread, and the damage sustained in areas that do burn. This study also demonstrates significant potential for changing fire regimes to drive large-scale, abrupt ecological change.

KEYWORDS
aerial photograph, annual grass, chaparral, drought, fire regime, grass-fire cycle invasive species, human development, predictive mapping, VTC, wildfire

INTRODUCTION

Rapid global change, such as shifts in fire regimes, has the potential to greatly disrupt ecological functioning and cause dramatic transformations. For example, once-dominant vegetation types may transition to different types and lead to cascading ecological impacts. A classic example of this is vegetation type conversion (VTC) from native woody shrublands to invasive annual grasslands in Southern California, one of the five Mediterranean-climate ecosystems in the world (Underwood, Franklin, et al., 2018). Chaparral shrublands provide a wide range of ecosystem services, and their support of exceptional species richness in one of the world's biodiversity hotspots makes their decline an issue of global significance (Rundel, 2018; Underwood, Hollander, et al., 2018).

The vulnerability of chaparral to high fire frequency—specifically, short fire return intervals—has been recognized in the literature and observed in field studies for many decades (e.g., Cooper, 1922; Haidinger & Keeley, 1993; Jacobsen et al., 2004; Keeley & Brennan, 2012; Zedler et al., 1983). However, the role of short-interval fire in driving type conversion has also been questioned in some studies (Meng et al., 2014; Storey et al., 2021). Once chaparral has been replaced with invasive grass, its recovery becomes unlikely, at least on human time scales (Anderson & Keeley, 2018; Zedler, 1995). Thus, better understanding of the rate, drivers, and potential locations of vulnerability is critical for identifying the most efficient and effective ways to prevent further decline.

Until recent years, empirical documentation on landscape scales of where and to what extent chaparral is being locally extirpated and replaced with herbaceous vegetation has been lacking. The few landscape-scale studies that have been conducted have only covered parts of chaparral's range in Southern California and have used different methodologies (e.g., Lippitt et al., 2012; Lucero et al., 2021; Meng et al., 2014; Storey et al., 2021; Syphard, Brennan, & Keeley, 2019a & b). Complicating our understanding is that these studies have found variation in the relative importance of factors most strongly correlated with woody chaparral decline and conversion to grass, particularly the role of short-interval fire.

For example, Meng et al. (2014) found a weak association between fire history and a remotely sensed index of vegetation cover. More recently, Storey et al. (2021) also reported that little evidence existed on the role of short-interval fire in effecting VTC, concluding that earlier studies demonstrating VTC were not typical of what was occurring over broad portions of the landscape. Lucero et al. (2021) found dynamic but generally weak evidence for the effect of a single, short interval between two successive fires on VTC, but they acknowledged the potential for spatial and temporal variation. On the other hand, landscape-scale studies by Lippitt et al. (2012), Syphard, Brennan, and Keeley (2019a & b) demonstrated that short-interval fire was an important factor separating sites of woody decline and VTC from those that did not change. Several factors likely play a role in accounting for the different conclusions about the role of short-interval fires in producing VTC. These studies examined different chaparral associations, and it is clear from field studies that shrub species are markedly different in terms of resilience to short-interval fires (Keeley et al., 2008; Schumann et al., 2020). The only VTC studies where species composition was considered was in the aforementioned field studies that followed species changes before and after short-interval fires.

An equally important factor are the different methodologies in landscape-scale VTC studies. Landscape studies that have implicated fire interval in explaining VTC were time-series studies of vegetation changes following a sequence of fires on a particular site; Lippitt et al. (2012) used field observations and Syphard, Brennan, and Keeley (2019a & b) used a time-series approach incorporating airphoto imagery to demonstrate changes in woody cover at particular sites in response to short-interval fires. In contrast, Meng et al. (2014) failed to find a fire-interval connection using Landsat remote-sensing indicators of plant biomass and took a so-called space-for-time approach in which, instead of demonstrating VTC at a single plot over time, they inferred it based on comparisons of paired plots with different fire histories. Lucero et al. (2021) also used paired plots, but instead of using Landsat data, they used fine-scale aerial imagery. These space-for-time studies assume that the only important difference between sites is the fire history; they control for certain types of environmental variation but cannot discern species composition. This is important in chaparral remote-sensing studies because of the complex mosaic of different species dominants (Peterson & Stow, 2003; Roberts et al., 1998), fine-scale environmental heterogeneity, and species distributions (Keeley, 2004). This chronosequence approach is fraught with problems and is not recommended for phenomena that can be studied by following changes on a site over time (Walker et al., 2010).

Understanding landscape changes requires a multivariate approach that considers factors other than fire interval. For example, Meng et al. (2014) found a reduction in vegetation cover after a short interval between fires at low elevations, and this likely was due to changes in community composition (i.e., chaparral is replaced at lower elevations by the smaller-stature sage scrub), as revealed by Lucero et al. (2021) and Syphard et al. (2006) and by the fact that human ignitions are inversely correlated with elevation (Keeley & Syphard, 2018a). Additionally, given the association of elevation with different plant communities and a range of physiological factors associated with plant growth or postfire recovery (Franklin, 1996), there could be multiple reasons for this pattern. Lippitt et al. (2012) observed a similar topographic effect with low elevation. Syphard, Brennan, and Keeley (2019a & b) found that other variables most strongly associated with VTC were indicators of soil moisture, which is consistent with Park et al. (2018), who found that the spatial distribution of herbaceous cover in chaparral communities was most strongly correlated with low soil moisture.

There are several ways that soil moisture availability may facilitate vegetation change. For example, drought-related plant mortality may drive chaparral decline and lead to VTC because dead shrubs open the canopy and allow for the establishment of sage scrub or invasive grasses (Jacobsen & Pratt, 2018). Drought may limit postfire recovery of chaparral and shift the competitive balance in favor of invasive grasses (Park et al., 2019). Also, the interaction between soil moisture and short-interval fires may play a role because obligate-seeding shrubs are most sensitive to short-interval fire and are also strongly favored on more arid sites (Keeley & Syphard, 2018b). Soil nitrogen is another factor that could increase the competitive ability of invasive species (Fenn, Allen, & Weiss, 2010); however, previous studies found it not to be a significant factor in postfire VTC (Keeley et al., 2005; Syphard, Brennan, & Keeley, 2019b).

An additional consideration is geographical differences in factors driving VTC. Understanding such variation might identify the variables of most concern in different regions; additionally, identifying the subregions most vulnerable could facilitate setting priorities in terms of where to focus decision-making and management. In this study, we expanded the geographical extent of previous empirical studies conducted with aerial photography to document and explain the relative extent and drivers of woody shrubland decline and conversion across Southern California. Our approach was spatially hierarchical, with separate analyses conducted across the entire area, by northern and southern regions, and by four subregions. This extended and hierarchical analysis enabled us to answer the following questions:

1. How much VTC has occurred across the entire Southern California region, and are there geographical differences in the amount of woody decline and conversion that are occurring?
2. What are the most important drivers or correlates to woody decline and conversion, and how do they vary across regions?
3. Do the geographical differences among regions result in different predictive model output maps of woody decline and conversion?

METHODS

Study region

The coastal region of Southern California is a hotspot of biodiversity that has already lost more than half of its area of natural vegetation due to habitat loss and fragmentation from urban development (Underwood et al., 2009), which continues apace (Radeloff et al., 2018). The region has a Mediterranean climate with cool, wet winters and hot, dry summers, and the most extensive vegetation types include the largely summer-deciduous sage scrub and taller-stature evergreen chaparral shrublands. Throughout the region these shrublands form a mosaic with oak woodlands, grassland, and, at higher elevations, montane conifer forests. The region is environmentally diverse with strong climatic and topographical gradients that vary from the coast to the interior and from the south to the north (Keeley & Syphard, 2018b).

The natural fire regime in the region is one of periodic high-severity crown fires that tend to be most destructive when driven by strong, dry, offshore Santa Ana winds (Faivre et al., 2016). Humans are responsible for at least 95% of fire ignitions, with lightning fires primarily restricted to the highest elevations in the interior mountain ranges (Keeley & Syphard, 2018a). Given the exponential population growth in the last century, wildfires have become uncharacteristically frequent, with extensive areas of chaparral having experienced fire return intervals much shorter than those from presettlement fire regimes (Safford & Van de Water, 2014). Although the area has a semiarid climate, prolonged periods of extreme drought can result in substantial vegetative effects (Dong et al., 2019).

To delineate the full study area, we selected two ecoregion provinces, California Coastal Chaparral Forest and Shrub and California Coastal Range Open Woodland

(Cleland et al., 1997), and constrained them to fall within San Bernardino, Santa Barbara, Ventura, Los Angeles, Riverside, and Orange Counties. We then subdivided the study area into northern and southern regions and four subregions. First, we used the ecoregion province boundaries to separate coastal from interior plots. However, there were no clear ecoregional or other boundaries separating the region into north and south. The metropolitan area of Los Angeles, California, however, creates a large gap between the sample plots to the north and south; we used this gap as a general dividing line, with State Route 330 creating the separation in the narrow interior area, where the northern and southern plots are relatively close together.

Airphoto imagery and random sampling

We previously created vegetation plots to analyze the drivers of VTC in San Diego County (Syphard, Brennan & Keeley, 2019b) and the Santa Monica Mountains (Syphard, Brennan, & Keeley 2019a). For the latter subregion, estimates of the amount of vegetation change could potentially have been biased by the intentional selection of plots in which woody cover had declined. Therefore, to estimate vegetation change across the entire study region considered here, we started with plot data from San Diego County ($n = 656$) and, using the same methodology, added new plots across the rest of the region, including the Santa Monica Mountains.

To generate the new plots, we selected and georeferenced the earliest available historical aerial photos ($n = 195$) from the University of California Santa Barbara Map and Image Library (http://mil.library.ucsb.edu/ap_indexes/FrameFinder) to cover the entire region (except for San Diego County). The historical photos were at the scale of 1:20,000, with dates ranging from 1943 to 1959. We subsequently acquired georeferenced overlapping contemporary photos (year 2019) with a resolution of 60 cm from the National Agriculture Imagery Program (NAIP) (https://gis.apfo.usda.gov/arcgis/rest/services) to pair with the historical photos for change analysis. Thus, the number of years between photos ranged from 60 to 76.

Across the photo coverage footprints, we generated 3411 random points spaced a minimum of 90 m apart in areas mapped as shrub in a historical vegetation map (Kelly et al., 2005). After deleting points overlapping imagery that was too poor to interpret, we generated 30-m buffers around the remaining points to create 0.28-ha plots for interpretation and analysis.

For all plots on both historical and contemporary images, we manually interpreted and recorded in four equal-interval numeric classes from 1 to 4 (corresponding to 0%–25%, 26%–50%, 51%–75%, and 76%–100%) the percentage cover of woody chaparral vegetation, herbaceous vegetation, and human disturbance (e.g., urban, agriculture, road, trail, or fuel break). We additionally recorded whether there were pure stands of each class (95%–100% cover) or whether the cover type was absent (0%–5% cover). We documented the type of human disturbance present in the plots for a summary of types of vegetation change overall. Although woody cover is easily distinguished from herbaceous cover in the imagery, we could not discern the condition of the chaparral in terms of drought-related dieback. However, even had there been dieback, the skeletons remained visible and were recorded as woody cover until the next fire. To ensure that postfire recovery was not mistaken for VTC, we deleted any plots that had experienced a partial or complete burn within 5 years of either image date, which is sufficient time for chaparral biomass to recover (Guo, 2001).

For all plots in which there was no recent fire, we recorded both gain and loss of woody cover over the study duration to show summary statistics of overall vegetation change (Table 1a). For statistical analysis of woody vegetation decline and conversion, we deleted plots in which there was less than 75% cover of woody vegetation or human disturbance in the earliest image date. This ensured that all plots started in the same condition and that our analysis was appropriately focused on decline or conversion. Also, because the focus of the statistical analysis was conversion of woody cover to herbaceous cover, we removed all plots that had become disturbed by human land use during the contemporary period. This ensured that the changes analyzed were vegetative changes only. We created two binary dependent variables. Woody decline included any plot in which chaparral had experienced at least a 25% conversion to grass (i.e., a cover decline of at least one class). For *type conversion*, the plot must have experienced more than 50% decline (i.e., a decline of at least two classes) such that herbaceous cover occupied more than half of the plot.

Explanatory variables

To determine the relative importance of potential drivers and environmental correlates with woody vegetation decline and type conversion to herbaceous cover, we used a suite of variables similar to prior studies (Syphard, Brennan, & Keeley, 2019a & b) (Table 1b). Previous work identified soil characteristics and water balance as important correlates with VTC and herbaceous expansion (e.g., Park et al., 2018; Syphard, Brennan, & Keeley, 2019a & b), in part because

TABLE 1 Description and native scale of (a) dependent and (b) explanatory variables used in statistical analysis of vegetation type conversion in Southern California from ∼1950 to 2019

	Description	Native scale and units
a) Vegetation change (dependent variables)		
Woody decline	Plot that was fully chaparral in historical period and experienced at least a 25% conversion to grass by contemporary period	30-m buffers around points (0.28 ha), binary
Woody conversion	Plot that was fully chaparral in historical period and converted to at least 75% grass by contemporary period	30-m buffers around points (0.28 ha), binary
b) Explanatory variables		
Soil and drought		
Actual evapotranspiration (AET)	Total annual water evaporated from surface and transpired by plants, assuming unlimited water, summed annually and averaged from 1981 to 2010	270-m raster, mm
Soil available water storage (SOIL_AWS)	Maximum amount of water available for plant use that soil can provide	30-m raster, mm
Nitrogen deposition	Annual deposition of reduced and oxidized nitrogen	Polygon converted to raster
Topography		
Elevation	US Geological Survey digital elevation model	30-m raster, m
Slope	Degree slope derived from elevation	30-m raster, degrees
Fire frequency		
Fire count	Total no. fires since 1878	Regions polygon converted to raster, count
Minimum fire return interval	Shortest no. years between any two fires on record or between contemporary image date (2019) and 1878, the first year in record	Regions polygon converted to raster, years
Fire departure	Estimated departure of contemporary fire return interval from median reference fire return interval of pre-Euroamerican settlement	Polygon converted to raster, percentage departure
Proximity to development or disturbance		
Distance to roads	Proximity to all TIGER line file roads, excluding 4WD and OHV roads. TIGER Roads 2015, US Department of Commerce, US Census Bureau	30-m raster, m
Distance to Wildland Urban Interface (WUI)	Euclidean distance to interface or intermix WUI in 2010	30-m raster, m
Terrestrial intactness	Relative natural condition of landscape as function of multiple types of human disturbance using input data from 2011 to 2015	Converted from polygon to raster, unitless (−1 to 1)

they mediate plant development and productivity. Therefore, we evaluated available soil water storage provided by the Natural Resources Conservation Service (https://www.arcgis.com/home/item.html?id=e66bffd8e4614cc9bf3c770fe6a4d4fc) and actual evapotranspiration (AET), calculated from topography, soil, precipitation, and temperature data produced by Flint and Flint (2012) using the California Basin Characterization Model (https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html). Because nitrogen deposition can moderate soil fertility and enhance the growth rates of invasive grasses (Fenn, Allen,Weiss, Jovan, et al., 2010), we used a 2002 map representing total annual deposition of reduced and oxidized nitrogen (kilograms of nitrogen per hectare per year) at 4-km resolution (Tonnesen et al., 2007). Topographical variables also have the potential to regulate energy and moisture balance (Franklin, 1995), in addition to mediating wildfire behavior directly, so we included elevation and slope as explanatory variables.

We considered two explanatory variables to capture the effect of fire frequency on vegetation change. For the first, minimum fire interval, we used the wildfire perimeter database from Cal Fire (https://gis.data.ca.gov/datasets/e3802d2abf8741a187e73a9db49d68fe_0), with overlapping fires mapped from 1878 to 2018. We overlaid all plots with the fire perimeters and calculated the minimum fire return interval as the shortest number of years between any two fires in the record that occurred before the contemporary image date (i.e., 2019). If no fire occurred in the record, we subtracted 1878 from the contemporary data year and used that as the minimum interval; if one fire occurred, we calculated the minimum interval to be the smaller of the interval in years been the fire date and either the beginning of the fire record or the contemporary data year. We considered, but ultimately did not use, the total count of fires as an explanatory variable because it was highly correlated with minimum interval. For the other variable, we used the USDA Forest Service fire return interval departure (FRID) map layer (https://www.fs.fed.us/r5/rsl/projects/gis/data/FRID/FRID_Metadata.html) to quantify the degree of difference between contemporary median fire return intervals at a site and the estimated fire return intervals that occurred in pre-Euroamerican settlement times. Although fires are burning less frequently than historical times in coniferous forests in California, the trend for much of the Southern California study area is for fires to be burning more frequently (Safford & Van de Water, 2014).

Because expansion of invasive grasses often results from their dispersal from disturbed areas (Fusco et al., 2021), we considered three metrics of human disturbance. Two of these, distance to roads (https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.2015.html) and Wildland Urban Interface (WUI) (http://silvis.forest.wisc.edu/data/wui-change/), were included in previous studies of type conversion in Southern California (Syphard, Brennan, & Keeley, 2019a & b) (Table 1). Here we also included a map that reflects the overall footprint of human disturbance on the landscape through a metric of terrestrial intactness (https://databasin.org/datasets/e3ee00e8d94a4de58082fdbc91248a65/).

We constrained the extent of all mapped variables to the study region and resampled all grids to the finest-resolution data at 30 m using the ArcMap (version 10.6.1) Resample tool with the Bilinear resampling technique (https://desktop.arcgis.com/en/arcmap/latest/tools/data-management-toolbox/resample.htm). We also converted all polygon layers to raster using the same extent and cell size. Around all plot points, we created a 30-m buffer, then extracted the mean value of all explanatory variables and assigned them to the plots. To simplify interpretation for evaluating variable importance, we charted results based on the variable with the highest percentage contribution to the model out of these groups: terrain (elevation and slope), disturbance (distance to roads and WUI and terrestrial intactness), soil (available soil water storage, AET, and nitrogen), and fire (minimum fire interval and fire departure).

Analysis

To quantify vegetation change, we summarized the number of plots in different woody and herbaceous cover classes for the historical and contemporary image dates. In addition to summarizing change across the entire study area, we also stratified the study region geographically to determine whether there were differences in the extent and drivers of vegetation change and whether those differences affected mapped predictions. Thus, we calculated these numbers and performed analyses separately for the northern and southern regions and for four subregions representing the combinations of north, south, coastal, and interior. Because sample sizes of full type conversion were small for the northern and southern coastal subregions ($n = 6$ and 9 respectively), we merged them with the interior regions in the north and south for inferential statistical analysis. For woody decline, however, we performed separate analyses for the four separate regions. For all explanatory variables, we quantified descriptive statistics, including minimum, maximum, average, and range of values for the explanatory variables for the four subregions (Phillips et al., 2006) of the study area to assess their relative environmental differences.

To quantify the relative importance of explanatory variables, we used two types of statistical analysis—one that estimated each variable's independent importance (hierarchical partitioning) using presence-absence data, and a presence-only multivariate analysis that accounted for variable interactions (MaxEnt, version 3.4.3, https://biodiversityinformatics.amnh.org/open_source/maxent/). Hierarchical partitioning is a statistical algorithm that calculates the isolated effect of each explanatory variable on the response, which in this case was binary, indicating either woody decline or woody conversion as presence and plots that did not change or decline as absence; for the MaxEnt modeling, we only used the presence data. The relative contribution of each variable is determined by running a hierarchical decomposition of a goodness-of-fit measure from regression models using all variable subsets (in this case a log-likelihood goodness-of-fit test for logistic regressions) (MacNally & Walsh, 2004). We used the hier.part package version 1.0–6 in RStudio (R Core Team, 2020).

For mapping and comparison of variable importance within a multivariate framework, we used the MaxEnt statistical software program (Phillips & Dudık, 2008) that was originally developed for species distribution modeling but has recently been used for a range of other ecological applications (Elith et al., 2010) and for mapping fire or ignition probability (e.g., Syphard, Rustigian-Romsos et al., 2019). One of the benefits of MaxEnt is its known high performance for spatial mapping, which is why we used that method for the mapping part of our work. MaxEnt performs well with small sample sizes (Hernandez et al., 2006; Oppel et al., 2012; Wisz et al., 2008), has high predictive accuracy compared to other modeling methods (Elith et al., 2006; Guisan et al., 2007; Shabani et al., 2018), and allows versatile and flexible settings that can account for model interactions and nonlinear relationships (Elith et al., 2006; Merow et al., 2013).

MaxEnt is a presence-only machine-learning algorithm that iteratively compares the differences in explanatory variables between locations of the response variable (here, the plot location of either woody decline or conversion) and the locations of a randomly generated sample of 10,000 background plots, located at least 30 m apart. Through these iterative comparisons, the model estimates the best approximation of the response variable environmental distribution as the one with maximum entropy. The model outputs a raster map in which an exponential function is used to assign each cell a value between 0 and 1 representing relative suitability. The model also generates metrics of variable importance and performance accuracy from the area under the curve (AUC) of receiver operating characteristic curves (Fielding & Bell, 1997).

For the MaxEnt modeling, we used the same predictor variables as in the logistic regression models and evaluated differences in variable importance in the different regions and subregions. We initially ran the models with all variables included to record their relative importance. The MaxEnt program produces two alternatives (Phillips et al., 2006) for assessing variable importance in this multivariate framework. The percent contribution reflects each variable's influence as the algorithm is fitting the model, whereas the permutation importance reflects the importance of each variable within the final model—done by iteratively removing each variable from the model and quantifying the decrease in model accuracy that results from the omission of that variable. In the models run with all variables, we focused on percent contribution as the metric of relative importance and provide permutation importance in the Supporting Information Appendix S1. After running the variable selection process, described in what follows, we focus on the permutation importance for the variables retained because these represent the final selected models used for mapping. MaxEnt used with default parameterization has been shown to result in overly complex models (Anderson & Gonzalez Jr., 2011; Moreno-Amat et al., 2015; Warren et al., 2014). Therefore, it is recommended that MaxEnt settings be tuned to optimize model complexity and performance (Merow et al., 2013). We took the following steps to reduce potential model overfitting: limited potential model complexity by constraining the feature types to linear, quadratic, and product; excluded correlated predictors from entering the same models; utilized an iterative stepwise variable selection process to increase model parsimony; and optimized the regularization multiplier.

Because we wanted to capture the spatial signature of vegetation change and not urban development, we restricted the training extent of the maps to all vegetated areas except medium-intensity developed, high-intensity developed, and cultivated crops, using the National Land Cover Database from 2016 (https://www.mrlc.gov/). Before running the models, we used ENMTools (version 1.4.4) (Warren et al., 2010) to calculate correlation coefficients between pairs of all variables, and none were correlated $r >= 0.7$.

After recording variable importance in the full models, we proceeded to conduct an iterative stepwise process of variable selection. For each iteration, we removed the variable contributing the least information to the model fit (highest mean training gain without the variable) to decrease model complexity and increase performance (Warren et al., 2014) and ran the model again with the remaining predictors. This was repeated until only one variable remained. The model with the fewest variables having a mean training gain not significantly different than the full model was selected for each. Significance was defined as a lack of overlap between 95% confidence intervals for training gain means (R Core Team, 2020). After variable selection, we then altered the regularization multiplier from 0.5 to 5 at 0.5 increments and used the Model Selection function in ENMTools to calculate the Bayesian information criterion (BIC) for each of the models (run with no replication and raw output). The final model was the one with the regularization multiplier producing the lowest BIC score. Finally, we ran a fivefold cross validation of the final model to assess model performance.

After completing this MaxEnt modeling process for the full region using both woody decline and woody conversion as the response variables, we repeated the process for the northern and southern regions. We also ran separate models for the four subregions, but only for woody decline due to the small sample size for full type conversion. Finally, we overlaid maps at these different spatial extents and then calculated and mapped the differences in predicted suitability for woody decline and conversion.

RESULTS

Extent of vegetation change

The total number of plots randomly sampled across the paired dates of air photos, including plots from the San Diego region (Syphard, Brennan, & Keeley 2019a), was 4067. From those we deleted 168 whose imagery was too poor to interpret, 326 that had had a fire within 5 years of either image date, and 833 plots that had had some type of human disturbance on either date. This resulted in a total of 2740 plots for which we analyzed vegetation change.

In terms of human disturbance, 741 out of 3899 (19%) plots were converted from vegetation to human land use over the study period. The reasons for natural vegetation conversion to human land use, from most to least common, included mechanical vegetation management (removal, thinning, and crushing of woody vegetation for linear fuel breaks) (31%), road development (26%), urban development (20%), trail construction (10%), miscellaneous agriculture (e.g., orchards, grazing, cropland) (8%), and undetermined (6%).

Most plots experienced no change in woody cover, and woody cover increased in some plots, particularly in the southern interior portion of the study area (Figure 1). Overall, there was a substantial net loss of

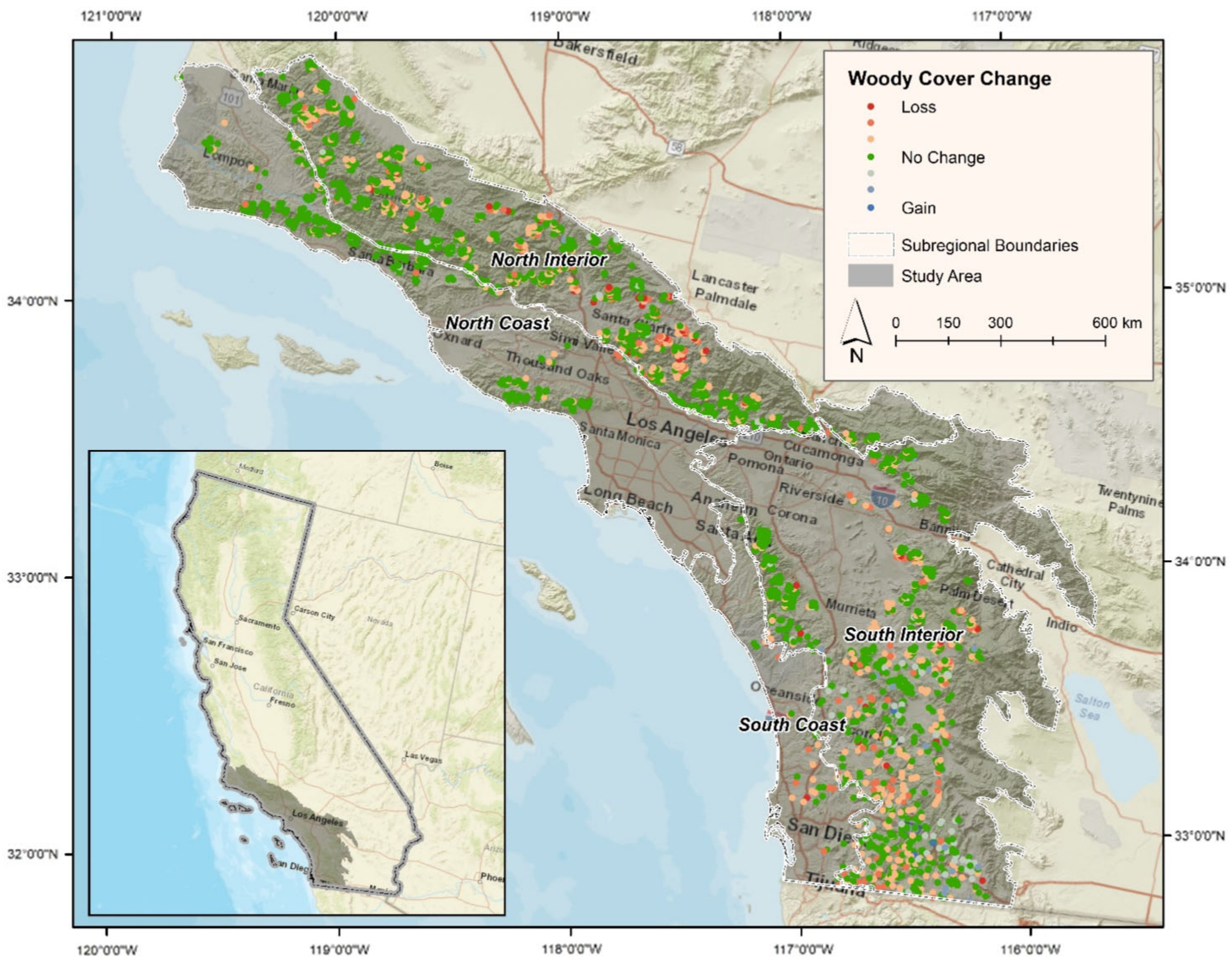

FIGURE 1 Study area map showing change in percentage woody cover from earliest to most recent image dates (~1950–2019) in Southern California. The middle value (green) indicates no change; the progressively warm colors display four classes of cover loss in 25% increments, with *woody decline* represented by all warm colors and *woody conversion* represented by the two darkest warm colors. The cool colors represent 25% increments of woody cover gain. The inset shows the study area location divided into four subregions.

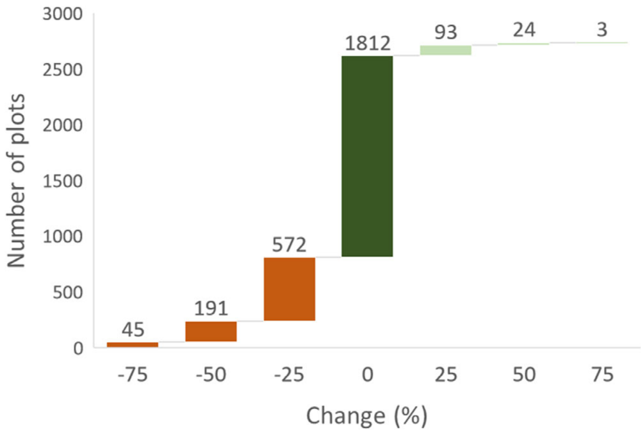

FIGURE 2 Net change in woody cover from earliest to most recent image dates (~1950–2019) in Southern California. Negative values indicate woody cover decline, and positive values indicate woody cover increase.

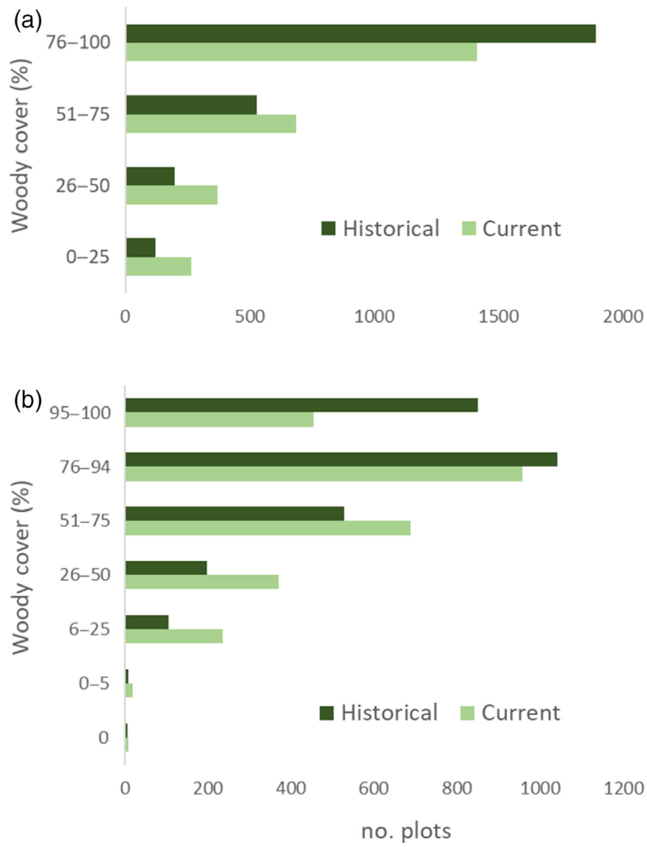

FIGURE 3 Number of vegetation plots distributed within woody cover classes in historical and current image dates show in (a) equal-interval classes of 25% cover and (b) equal-interval classes plus classes of pure woody (95–100%) and pure herbaceous (0–5%) vegetation

woody cover across the study region (Figures 1 and 2), along with herbaceous expansion (Appendix S1: Figure S1). The most dramatic decline was in the cover of originally pure stands of chaparral (i.e., 95%–100% woody cover) (Figure 3). When separated into subregions, both southern areas experienced the largest proportion of woody decline and conversion, most in the south coast (Figures 1 and 4), although the south coast had the smallest number of plots in the four regions. In the northern region, the interior experienced more woody vegetation decline and conversion than the coastal area (Figures 1 and 4).

Drivers of vegetation change

There were differences in the distribution of explanatory variables among the regions and subregions of the study area (Table 2, Appendix S1: Table S1). The coastal regions were less rugged and lower in elevation than the interior regions. The southern region showed the highest presence of human development, with shorter overall proximity to roads and the WUI, and both coastal regions were more highly disturbed than the interior regions. Available soil water storage and AET were generally higher in the north than the south, although soil water storage was lowest in the northern interior region. Nitrogen content in the soils was highest in the coastal regions. The shortest minimum fire interval was in the northern interior, but the largest departure in fire intervals was by far in the southern coastal area. In all areas, the average fire departure was negative, indicating that fires are overall more frequent than they have been historically.

Across the full region and in the north and south, fire was most frequently ranked as the most important variable (Figure 5, Appendix S1: Figures S2–S13) for woody decline and conversion. This was true both in terms of independent contribution through hierarchical partitioning and in terms of percent contribution in multivariate MaxEnt modeling. However, in the hierarchical partitioning models, the independent contribution of fire in the full region was less important than AET for both woody decline and conversion; and fire was also less important than slope for woody decline (Figure 5b, Appendix S1: Figure S2). In the MaxEnt models in which all variables were compared, both minimum fire interval or fire departure were the most important variables regionwide as well as in the north and south (Figure 5b, Appendix S1: Figures S2 and S3). Variable rankings among the other three classes of variables showed no clear trends and shifted slightly depending on whether the model was for woody decline or conversion or depending on the measure of variable importance.

In models fit with all explanatory variables in the subregions, fire again was ranked highest most frequently, but terrain and soil-related variables were more important compared to the models fit at larger extents (Figure 6a,b, Appendix S1: Figures S2–S13). In the hierarchical partitioning models, terrain (in this case slope [Appendix S1: Figure S1]) was ranked almost equally as fire for the coastal areas; and for the south interior, both slope and AET were more important than fire, albeit only slightly (Figure 6a, Appendix S1: Figure S2). In the multivariate MaxEnt models, soil (in this case nitrogen deposition [Appendix S1: Figure S3]) was nearly as important as fire interval in the north coast; and in the south coast, potential soil moisture in terms of available water storage and elevation were both slightly more important than fire (Figure 6b, Appendix S1: Figure S3). In the subregional models, human disturbance variables were generally less important than the other variable types (Figure 6a,b), although there was substantial variation among individual variables (Appendix S1: Figures S2 and S3).

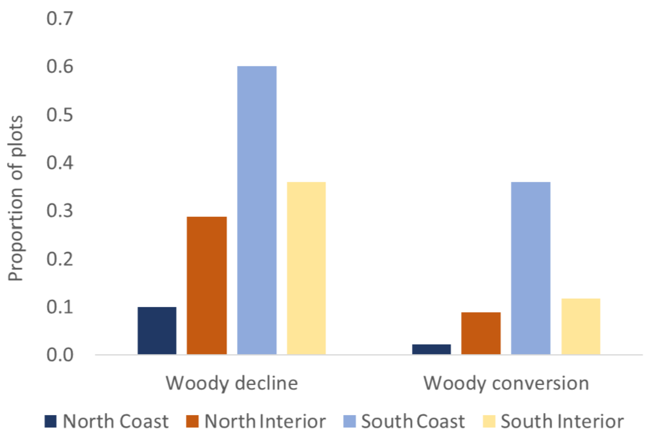

FIGURE 4 Proportion of plots experiencing woody decline and conversion from earliest to most recent image dates (~1950–2019) in four subregions of Southern California

After variable selection and model fitting, all multivariate MaxEnt models for woody decline and conversion and across all regions and subregions retained minimum fire return interval as the highest-ranking variable (Tables 3 and 4). For the full region, elevation and AET were both retained for both woody decline and conversion, and for woody decline, terrestrial intactness was the second-ranking variable in permutation importance. Terrestrial intactness was also the second-ranking variable for woody decline in the north and south but was only retained in the model for the northern region for woody conversion. For woody decline, distance to WUI was retained for the north and distance to roads was retained for the south. Distance to roads was also the third-ranking variable for woody conversion in the south.

For the subregional MaxEnt models of woody decline after variable selection, fire interval was the only variable retained in the best models for the two coastal regions. In the northern interior, elevation, terrestrial intactness, distance to WUI, and nitrogen were also retained. In the southern interior, terrestrial intactness, AET, distance to roads, and slope were retained.

The AUC for both training and test data sets ranged from 0.7 to 0.79 for all models except the model on test data for woody conversion in the south, which was 0.52, with the training AUC at 0.79 (Tables 3 and 4). The regularization multiplier that resulted in the lowest BIC score varied across the models from 0.5 to 4.5.

TABLE 2 Average values for predictor variables explaining woody decline and conversion in Southern California

	Unit	Full region	North	South	North coast	South coast	North interior	South interior
Elevation	m	726.6	693.6	758.7	230.0	166.8	1137.0	876.9
Slope	Degrees	13.5	14.9	12.2	9.1	8.7	20.4	12.9
Distance to roads	m	793.9	817.0	771.5	253.2	278.2	1356.4	870.1
Distance to Wildland Urban Interface (WUI)	m	3239.4	4294.7	2213.1	3412.4	1551.7	5138.8	2345.2
Terrestrial intactness	Metric, −1 to 1	0.1	0.1	0.1	−0.4	−0.4	0.5	0.2
Available soil water storage	mm	102.6	113.9	89.3	149.4	97.5	81.3	87.4
Actual evapotranspiration	mm	316.5	330.6	302.8	346.0	302.7	315.9	302.9
Nitrogen	kgN_ha_year	9.7	10.0	9.4	12.7	10.6	7.5	9.1
Fire count	Sum	1.1	1.2	1.0	0.8	1.0	1.7	1.0
Fire interval	Years	74.9	70.5	79.2	99.2	85.1	43.0	78.1
Fire departure	Percentage	−10.9	−11.6	−10.3	−13.0	−32.2	−11.0	−8.1

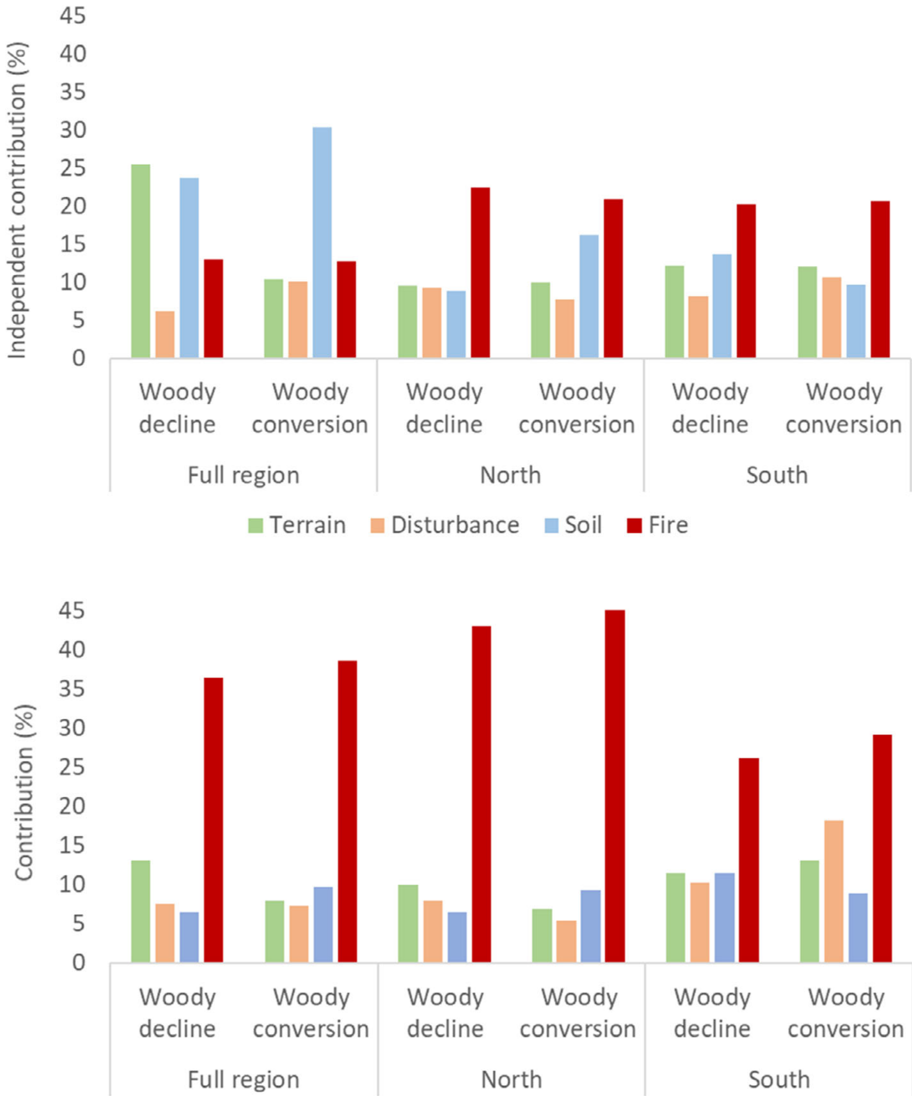

FIGURE 5 Relative importance of variable classes explaining woody decline and conversion in north, south, and full Southern California regions using (a) hierarchical partitioning and (b) MaxEnt models (for ungrouped variable results, see Appendix S1: Figure S1)

Distribution maps of suitable conditions for woody decline and conversion

Across the entire region, the areas mapped as having the highest potential for woody decline were similar to those with the highest potential for woody conversion. Areas of the highest likelihood of vegetation type change were distributed in the same general locations with slight discrepancies in probability (Figure 7).

When comparing maps from regionwide models to maps developed separately for the north and south, there was better correspondence with maps of woody decline (mean $r = 0.91$) than conversion (mean $r = 0.86$), and there was better correspondence with maps developed for the north ($r = 0.97$ for woody decline and $r = 0.91$ for woody conversion) than for the south and regionwide (0.85 for woody decline and 0.81 for woody conversion) (Figure 8a,b, Table 5). The differences in the maps of woody conversion were most extensive in the southern coastal part of the landscape, where the maps developed at smaller spatial extents predicted a higher probability of conversion than the regionwide map. For woody decline, the differences between maps showed no clear spatial trends, although the smaller-extent maps generally predicted higher probabilities near the coast and the regionwide map generally predicted higher probabilities in the interior (Figure 8a,b).

When maps developed for the four subregions were compared to maps developed regionwide (Figure 8c) or to maps developed for the north and south (Figure 8d), there was overall better agreement between subregional maps and the north and south maps than there was between subregional maps and the regionwide map (Figure 8c,d, Table 5). There was also a stronger

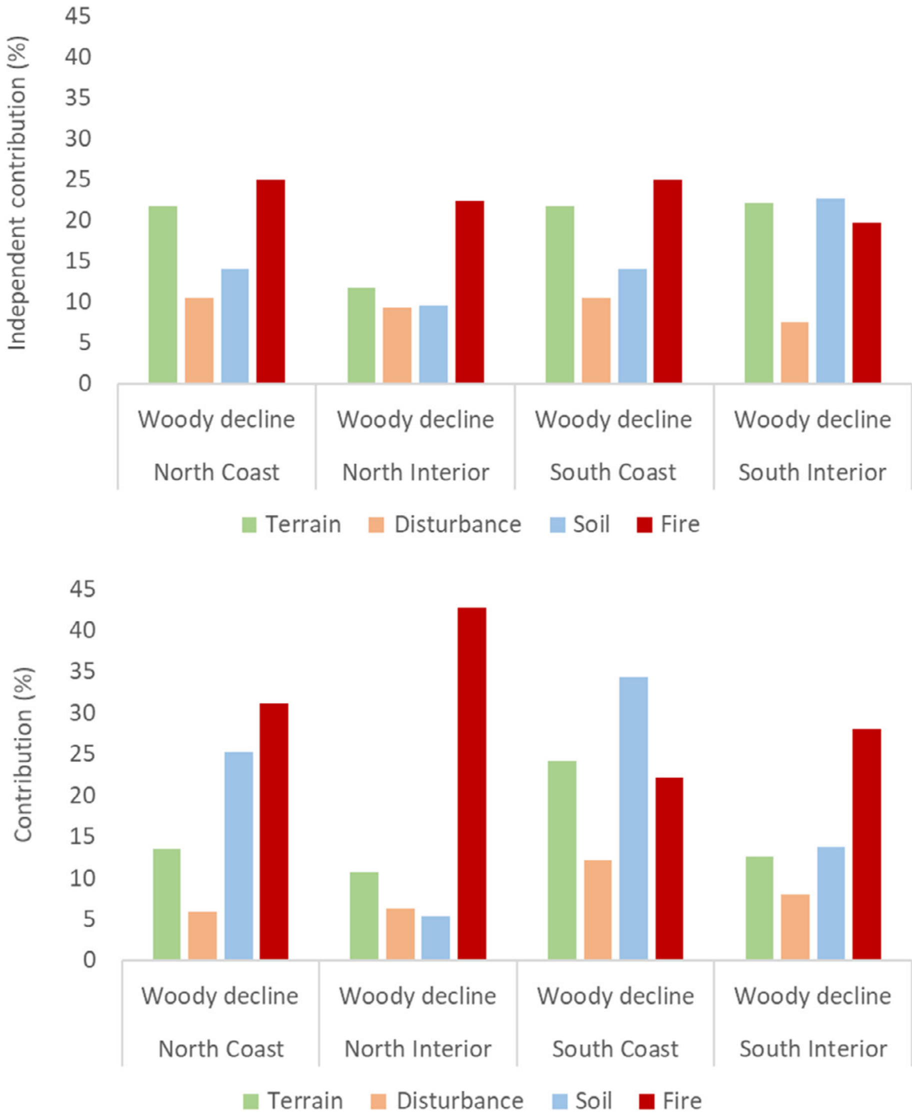

FIGURE 6 Relative importance of variable classes explaining woody decline and conversion in four Southern California subregions using (a) hierarchical partitioning and (b) MaxEnt models (for ungrouped variable results, see Appendix S1: Figures S2–S3)

correlation in the interior regions than in the coastal regions (Table 5), with coastal subregions tending to predict higher probabilities of vegetation change than interior regions (Figure 8c,d).

DISCUSSION

Widespread decline of woody chaparral shrubland vegetation and replacement with invasive grass has the potential to dramatically reduce ecological functioning and provision of ecosystem services in Southern California, with global implications in terms of rapid vegetation shifts in other fire-prone regions. Although previous work across shorter spatial or temporal extents has generated disagreement over the extent of this change and the reasons for it, our analysis across Southern California shows that decline of woody shrubs and conversion to grass has occurred extensively, with highest proportions of change in the northern interior and southern coast. Variables related to short-interval fire were most frequently ranked highest in predictive importance, but there was geographical variation across regions, as reflected in mapped output from distribution models.

We used several ways of quantifying variable importance in explaining woody decline and conversion, including independent contributions from binomial regressions and joint contributions from multivariate MaxEnt models—for seven different spatial extents and for both woody decline and conversion. For 16 out of the 20 different models comparing independent variable contributions (Figures 5 and 6), fire-related

TABLE 3 Explanatory variables giving their permutation importance and evaluation statistics for multivariate MaxEnt models of woody decline and conversion for regionwide models and models for north and south. The permutation values range from 0 to 100, with higher values representing greater importance in explaining vegetation change

	Woody decline			Woody conversion		
	Full region	North	South	Full region	North	South
Fire interval	58.1	60.7	41.8	73.6	87.2	58
Terrestrial intactness	23.7	19.1	25.1	...	4.2	...
Elevation	11.3	17.5	...	13.2	8.6	...
Actual evapotranspiration (AET)	6.8	...	20.5	13.2	...	22.8
Distance to Wildland Urban Interface (WUI)	...	2.7	...	...	...	...
Distance to roads	...	...	12.6	...	...	19.1
Sample size	539	295	244	173	89	84
Regularization multiplier	4.5	4	2	2.5	2.5	2
Mean test area under curve (AUC)	0.74	0.76	0.76	0.76	0.74	0.52
Mean train AUC	0.74	0.77	0.77	0.77	0.76	0.79

TABLE 4 Explanatory variables, permutation importance, and evaluation statistics for multivariate MaxEnt models of woody decline for subregional models in Southern California

	North coast	North interior	South coast	South interior
Fire interval	100	60.5	100	41.6
Elevation	...	17.9	...	...
Terrestrial intactness	...	8.5	...	20.8
Distance to WUI	...	6.7	...	...
Nitrogen	...	6.5	...	...
Actual evapotranspiration (AET)	...	...	...	19.9
Distance to roads	...	...	...	12.5
Slope	...	...	...	5.1
Sample size	28	267	15	230
Regional multiplier	0.5	4.5	0.5	1.5
Mean test area under curve (AUC)	0.72	0.7	0.74	0.76
Mean train AUC	0.72	0.71	0.74	0.78

variables were ranked as more important than other variables. The exceptions were the regression models performed regionwide for woody decline and conversion, where soil water storage (woody decline and conversion) and terrain (woody decline) were higher ranking; the regression model for woody decline in the southern interior, where soil water storage and terrain both ranked slightly higher; and for woody decline in the southern coast, where again soil water storage and terrain ranked slightly higher. In the multivariate models, not only was fire interval retained in all models after variable selection, but it was also the top-ranking variable in all models, with it being the only variable retained for the northern and southern coast models of woody decline.

Although both Meng et al. (2014) and Storey et al. (2021) have questioned the role of short-interval fire in explaining VTC in chaparral, and Lucero et al. (2021) found weak evidence for it, the results here overwhelmingly point to short-interval fire and the degree of departure from historical fire return intervals as most important—regardless of the modeling method used or spatial extent of analysis. It is noteworthy that we used here a variable that has not been explored in other work, including our own previous studies—the measure of fire interval departure (vs. minimum fire interval). Estimates of departure in this metric are mapped as a function of current fire return intervals compared to historical estimates for 28 different vegetation types (Safford & Van de

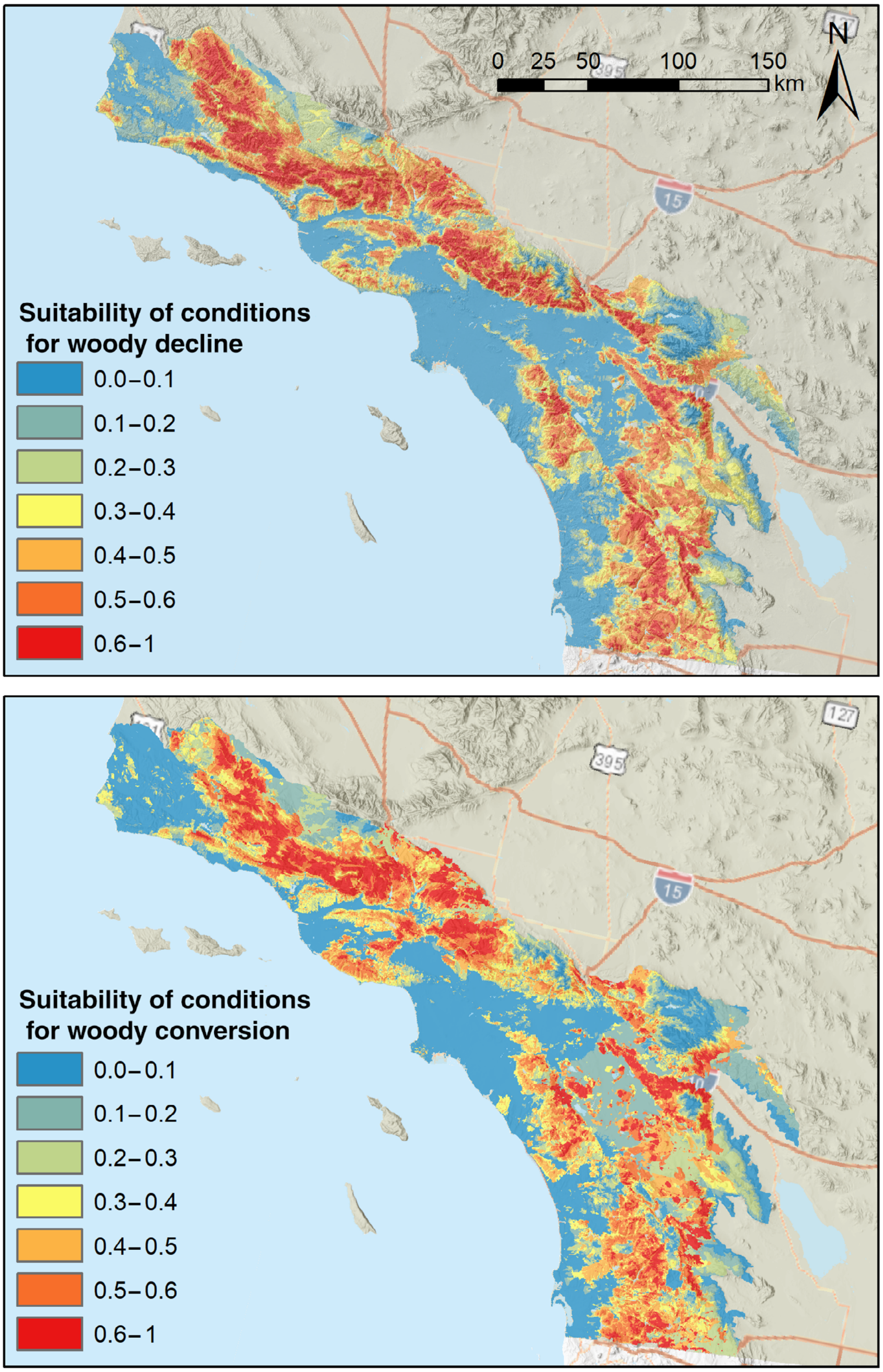

FIGURE 7 Distribution of areas with most potential for woody decline or conversion across Southern California

Water, 2014). This variable was frequently more important than minimum fire interval in the independent measures of variable importance (Appendix S1: Figures S1 and S2). Given its association with vegetation type, therefore, it is possible that in some cases it reflects species composition and picks up a stronger correlation with vegetation change than fire-related variables used in other studies. Species composition plays a large role in vulnerability to frequent fire owing to the nature of regeneration. For example, obligate seeding species, which depend on building a seed reserve in the soil that is sufficient to ensure postfire survival, pass through a prolonged growth period of up to 20 years in which seed production is minimal or zero. They are therefore vulnerable to short periods between fires, which can kill them before they have established a sufficient seed reserve (Haidinger & Keeley, 1993; Keeley, 1991; Keeley & Brennan, 2012).

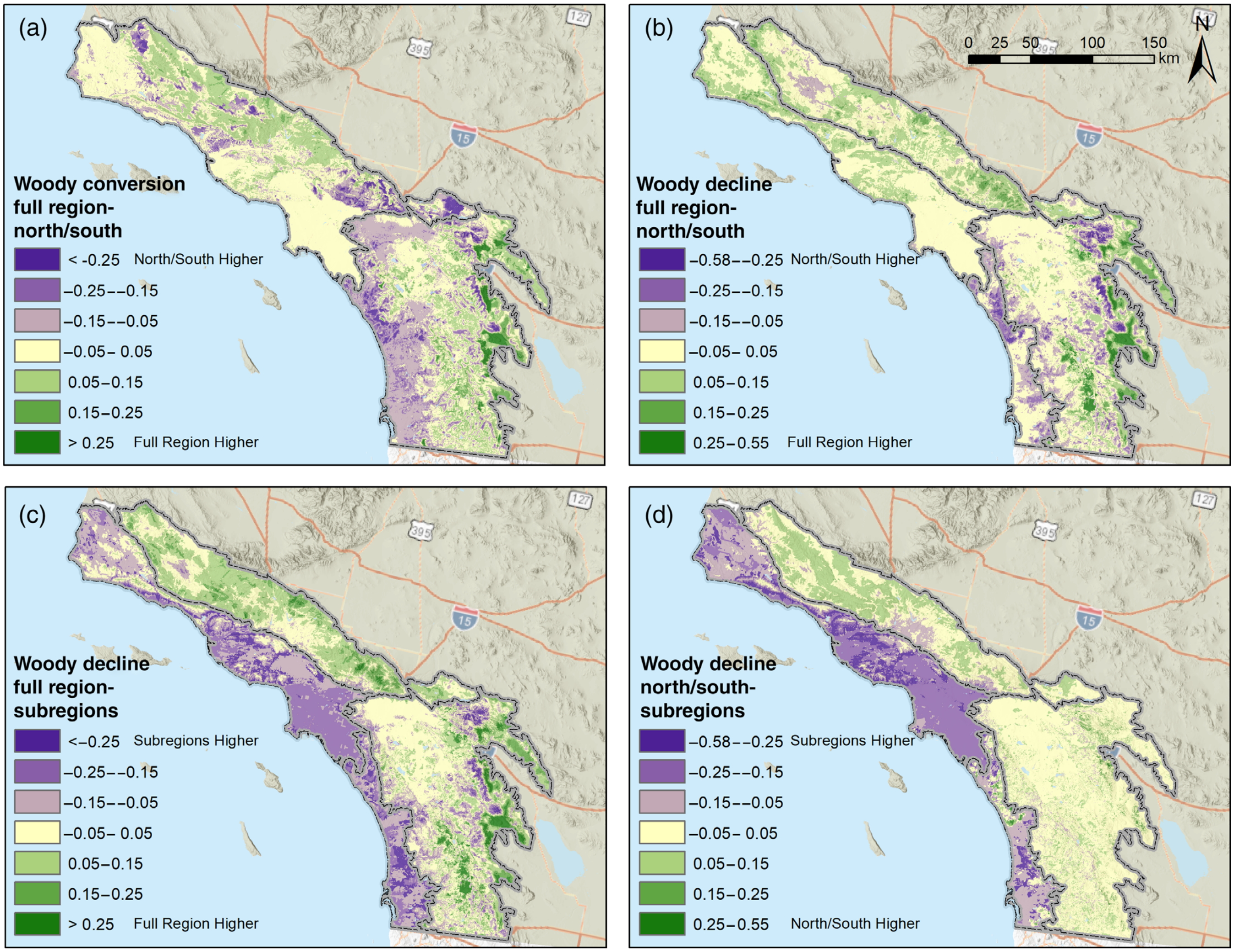

FIGURE 8 Differences in suitability for potential (a) woody conversion to herbaceous between MaxEnt models developed across full region versus models developed separately for northern and southern areas, (b) woody decline between MaxEnt models developed across full region versus models developed separately for northern and southern areas, (c) woody decline between MaxEnt models developed across full region versus models developed separately for four subregions, and (d) woody decline between MaxEnt models developed for northern and southern areas versus models developed separately for four subregions

TABLE 5 Correlation coefficients among maps produced from models of woody vegetation decline and conversion developed across different spatial extents in Southern California

	Woody decline			Woody conversion
	Regionwide	North	South	Regionwide
North	0.97	...	...	0.91
South	0.85	...	...	0.81
North coast	0.87	0.85	...	...
North interior	0.91	0.95	...	...
South coast	0.83	...	0.81	...
South interior	0.84	...	0.98	...

Another potential reason that other research found weaker relationships between fire and chaparral decline is that those studies isolated areas that had reburned a set number of times (i.e., once or twice) within a shorter temporal extent of analysis. In this study, fires could have burned frequently over a longer period across a larger geographical area, and that may be important in terms of the process of type conversion. Type conversion is a gradual, long-term process that often occurs as a function of multiple disturbance events over time in areas that are environmentally vulnerable to this change. That is, it may take more than one or two short fire-interval events for significant change to occur, and the number of events that trigger this change likely vary by region as a function of species composition and environmental context.

For type conversion to occur, several processes are involved. Initially, the aboveground portions of adult shrubs are killed, typically via wildfire, but potentially also because of drought. Subsequently, another fire may kill the seedlings or resprouts before they fully recover, which is why the immediate driver is often short intervals between fires. In addition to having sufficient time for regeneration, environmental context is important relative to successful recovery, and this is the most likely explanation for the strong correlation of woody decline and conversion with factors such as drought and topography–and for the geographical variation in relative variable importance. Soil aridity, which is perhaps best captured by AET, was a very significant factor in both woody cover decline and conversion to herbaceous vegetation (Appendix S1: Figures S1 and S2), although the relationship was nonlinear, with VTC most likely at intermediate to high levels of AET but then dropping at the highest AET values. This is likely operating in conjunction with fire because increased soil aridity in the immediate post-fire years is detrimental to shrub seedling survival and favors annual grasses, which can further deplete soil moisture (Davis & Mooney 1985). Soil aridity also favors obligate seeding shrubs (Davis & Mooney 1985), and this functional type is highly sensitive to short-interval fires; thus, the association of VTC with soil aridity may in reality be a result of frequent fires.

Another possible reason for the differences in results between our studies and those of Meng et al. (2014) and Lucero et al. (2021) is that our approach used a historical view of changes over time and theirs relied upon paired plots and a space-for-time substitution. That is, we directly tracked change at one site over time, whereas the other studies inferred change by comparing two sites with different fire histories and then attributed the change to the fire. Though the other studies attempted to control for environmental differences between plots, resource gradients and species composition are highly heterogeneous in many parts of Southern California, particularly in rugged areas where topoclimate variability may be as fine scale as <10 m (Ackerly et al., 2010). Given the strong influence of topoclimatic diversity on plant species' distribution and abundance (Franklin, 2010), this is an additional source of uncertainty in determining whether one plot in a pair can accurately substitute for another (Walker et al., 2010).

Geographical variation in factors that influence species distribution, composition, and abundance also potentially explains why it has been difficult to assess the extent and drivers of VTC in Southern California. Although the high ranking of fire interval was consistent across regions and spatial extents, its relative importance in combination with other environmental variables did vary, and these variations were reflected in the mapped predictions of potential VTC hotspots. In other words, maps created at smaller spatial extents reflect the unique geographical combination of factors best explaining the footprint of vulnerability in that region. When models are conditioned at larger geographical extents, they average the regional or subregional relationships, resulting in more generalized models.

Maps illustrating areas with the highest potential for vegetation change could be critical for determining management or restoration priorities; thus, mapped differences may have important consequences. The largest discrepancy in maps was in the southern part of the region, particularly along the coast. The maps developed in the northern coastal area also differed substantially from the maps conditioned at larger spatial extents. Overall, the southern part of the region experienced more decline and conversion than the north, which may partly explain the larger disagreement in mapped model output. On the other hand, the northern coast experienced the smallest vegetation change of the four subregions.

At least for the coastal areas, the most likely explanation for map differences is that the most accurate and simple subregional models only retained fire interval as the explanatory variable. Although our model selection approach is widely advocated for balancing goodness of fit with the potential for overfitting models, in this case the models may be underfit. In terms of decision-making, it may be desirable to have some balance between capturing regionally specific relationships (i.e., the subregions) with some of the generality reflected in maps at larger extents. The maps developed separately for the north and south may therefore serve most effectively for guiding decisions, although new maps could be developed for other geographies of interest, such as coastal or interior. While these maps illustrate the conditions that most closely approximate those where VTC has occurred, there is uncertainty inherent in where change may occur in the future. Also, the performance of the models was only slightly above average (AUCs mostly ranging from 0.7 to 0.8) (Fielding & Bell, 1997). Although fires do tend to recur within the same geographical areas (such as wind corridors) in Southern California, it is possible that short fire return intervals may occur in different types of areas in the future. Accounting for species composition is also critical for assessing VTC potential in Southern California, and these maps do not account for that.

Of the three general types of variables—fire, terrain, and proximity to human infrastructure—proximity to human infrastructure was never the top-ranking variable, despite its significance in many models. The spread of invasive grasses throughout the landscape often occurs unintentionally along roads, trails, powerlines, or other human land uses (Vila & Ibáñez, 2011). Thus, while these anthropogenic variables would not directly contribute to chaparral decline or recovery, they could account for the proximal source for grass dispersal and establishment (Fusco et al., 2021). Contrary to this expectation, however, the relationships here were counterintuitive such that VTC was more likely to occur at longer distances to roads or the WUI and in areas that were relatively more intact. The likely reason for this is that, given the strong association with wildfire, VTC may be more likely to occur in remote or continuous vegetation because these places are where larger fires are able to spread. Other research has shown that, though ignition probability is highest adjacent to human infrastructure, area burned tends to have an inverse relationship and tends to be largest far from roads or populated places (e.g., Syphard, Rustigian-Romsos, et al., 2019). This suggests that the detrimental effect of short-interval fire on chaparral overrode the positive effect of human adjacency as a source of grass.

In conclusion, this study shows the overwhelming importance of changes in fire regimes in causing VTC from shrublands to grasslands. Abrupt changes in fire regimes have the potential to upset ecological structure and function across a wide range of ecosystems and are considered a major global problem (Pausas & Keeley, 2014). In fact, VTC among diverse vegetation types is occurring globally as a result of sudden fire regime shifts (e.g., Coop et al., 2020; Fernandes, 2013). In Southern California, where the primary issue is frequent fire, the management approach of prescribed fire could exacerbate this vegetation shift with little effect on subsequent burning (Price et al., 2012). On the other hand, given that the primary cause of short-interval fires is human ignitions (Keeley & Syphard, 2018a), fire prevention has the potential to be the most cost-effective management approach.

CONFLICT OF INTEREST

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government.

DATA AVAILABILITY STATEMENT

Data are available in Data Basin at https://databasin.org/galleries/aea3ce47dd874848a69bec856400bba3/#expand=297919%2C297920.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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